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Biogeographical scenarios modulate seagrass resistance to small-scale perturbations

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Abstract 1. Seagrasses constitute a key coastal habitat worldwide, but are are exposed to multiple perturbations. Understanding elements affecting seagrass resistance to disturbances is critical for conservation. Distinct biogeographical scenarios are intrinsically linked with varying ecological and evolution backgrounds shaped across millennia.

2. We addressed whether the resistance (change in shoot abundances) and performance (change in leaf morphology and growth) of the seagrass *Cymodocea nodosa* to a local stressor, light reduction, varied across three regions (Southeast Iberia, the Balearic Sea and the Canaries) within the temperate northern Atlantic realm. We hypothesized that distinct biogeographical scenarios, in terms of distinct ecological/environmental conditions and genetic diversity of meadows, would affect seagrass resistance and performance, with flow-on effects on associated epifauna. The same experiments, in terms of shading intensities, timing and duration, were replicated at three seagrass meadows within each region.

3. Results demonstrated inter-regional variation in the resistance and performance of *C. nodosa*. Under moderate and high shading, shoot abundance was abruptly decreased, relative to controls, in the Canaries with concurrent, but less accentuated, changes in leaf morphology and no changes in growth. In the other two regions, however, moderate and high shading had a negligible effect on shoot abundance, leaf morphology and growth. Shading had no overall effect over the total abundance and assemblage structure of epifauna; these faunal attributes,

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however, varied between regions. Low seagrass resistance at the Canaries is linked with the peripheral distribution of the species there, favoring isolation and decreased genetic diversity.

4. *Synthesis*. Different biogeographical scenarios shape seagrass resistance to local perturbations. From a conservation perspective, if resistance differs among biogeographical scenarios, universal conservation rules for seagrasses are challenging.

KEYWORDS coastal habitats, impacts, macroecology, resilience

Resumen 1. Las angiospermas marinas constituyen un hábitat prioritario globalmente, pero están expuestas a múltiples perturbaciones. Comprender qué elementos afectan su resistencia a impactos es crítico para la conservación. Distintos escenarios biogeográficos están vinculados con distintos contextos ecológicos y evolutivos modulados durante milenios.

2. Evaluamos si la resistencia (cambio en abundancias de haces) y funcionamiento (cambio en la morfología foliar y crecimiento) de la angiosperma marina *Cymodocea nodosa* a un estresante local, reducción luminosa, varió entre tres regiones (sudoeste de la Península Ibérica, Mar Balear e Islas Canarias) en el Atlántico norte. Nuestra hipótesis es que distintos escenarios biogeográficos, en cuanto a distintas condiciones ecológicas/ambientales, así como de diversidad genética de las praderas, afectaría la resistencia y funcionamiento de la angiosperma, con efectos sobre la epifauna asociada. Los mismos experimentos, en términos de intensidad de sombreado, tiempo y duración, se replicaron en tres praderas de cada región.

3. Los resultados demostraron variación entre regiones en la resistencia y funcionamiento de *C. nodosa*. Bajo sombreado moderado e intenso, la abundancia de haces decreció abruptamente, en relación con controles, en Canarias, con cambios menos acentuados en la morfología foliar y ausentes para el crecimiento. En las otras dos regiones, sin embargo, el sombreado moderado e intenso tuvieron un efecto despreciable sobre la abundancia de haces,

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morfología foliar y crecimiento. El sombreado no tuvo efecto sobre la abundancia total y estructura multivariante de la epifauna, que variaron no obstante entre regiones. La baja resistencia en Canarias se vincula con la distribución periférica de la especie allí, lo que favorece el aislamiento y una diversidad genética baja.

4. Síntesis. Diferentes escenarios biogeográficos afectan la resistencia de la angiosperma a perturbaciones locales. Desde una perspectiva de conservación, si la resistencia difiere entre escenarios biogeográficos se hace difícil disponer de reglas de conservación universales para las angiospermas marina.

1. INTRODUCTION

Seagrasses worldwide constitute a key habitat on coastal soft bottoms, where they profoundly influence their physical, chemical and biological environment, acting as 'ecological engineers', and provide numerous 'goods and ecological services' to humans (York et al. 2017). Seagrasses are exposed to different types of human-induced disturbances, which frequently leads to habitat fragmentation and loss and even local/regional extirpation. In fact, large-scale seagrass losses have been reported from many coastal areas, mainly due to intense human-related activities, which has caused a worldwide declining trend (Waycott et al. 2009).

Resilience is the self-organization capacity of a system after a perturbation to maintain its identity and function (Gunderson et al. 2010). Ecosystem resilience encompasses both resistance, as the ability to persist during adverse conditions (Levin and Lubchenco 2008), and recovery once these adverse situations cease. In this context, seagrass resilience incorporates both resistance to, and recovery from, perturbations (Kilminster et al. 2015, O'Brien et al. 2017, Barry et al. 2018). Traditionally, seagrass resilience, including

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resistance, has been considered as species/genus-specific according to species/genus traits. Some seagrass species/genus are more resistant than others, while other seagrasses recover faster following perturbations (Erftemeijer & Lewis 2006, Kilminster et al. 2015, Roca et al. 2016, O'Brien et al. 2017, York et al. 2017). Resilience capacity of seagrass species has even been recently adopted to functionally classify seagrass species (Kilminster et al. 2015). However, local-scale environmental conditions (e.g. light regimes, wave action, etc.), in conjunction with the demographic history and genetic variation at the meadow scale, can affect resistance within species. For example, the existence of a large and diverse number of genotypes within meadows provides an ideal scenario for adaptation to, and recovery from, environmental stress (Salo et al. 2015), including reduced light levels (Evans et al. 2017). Reductions in light availability are one the main perturbations affecting the physiology and overall fitness of seagrasses worldwide (Leoni et al. 2008); decreased shoot survivorship and altered vegetative development can consequently affect associated epifauna (Gartner et al. 2010).

The biogeographical context considerably affects the phenology of certain seagrass species (Blok et al. 2018). However, variation across biogeographical scales has been largely overlooked as an element driving resistance to local-scale impacts of seagrass species (Fraser et al. 2014, Barry et al. 2018, Jahnke et al. 2018). Not surprisingly, experimental approaches to tackle resistance of 'ecological engineers', e.g. seagrasses, to varying perturbations have followed the traditional reductionist perspective of setting up experiments at local scales, i.e. at the patch scale in the case of seagrass meadows (Leoni et al. 2008). While biogeographical comparisons do not allow for inferences of causality, distinct biogeographical scenarios are intrinsically linked with varying ecological, environmental and evolutionary scenarios shaped across millennia (Siqueira et al. 2016) that will likely influence resilience. For example,

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phylogeographic differentiation of the seagrass *Zostera marina* affects long-term adaptation of this seagrass to warming stress (Jueterbrock et al. 2016).

Cymodocea nodosa (Ucria) Ascherson is a seagrass distributed throughout the entire Mediterranean Sea and the adjacent eastern Atlantic coasts, including the Macaronesian archipelagos of Madeira and the Canaries (Alberto et al. 2006, Cunha and Araújo 2009, Mascaró et al. 2009, Tuya et al. 2014a), providing food and shelter for diverse invertebrates and fish assemblages (Espino et al. 2011, Tuya et al. 2014b). From an evolutionary point of view, this seagrass originated in the eastern Mediterranean by divergence from its close relative in the Indian Ocean, and colonized the western Mediterranean and Atlantic by spreading westwards (Masucci et al. 2012). In the Canary Islands, the evolution of *C. nodosa* has followed a 'founder effect', whereby all genotypes derived from a few initial colonizers (Alberto et al. 2006). Populations from the Canary Islands constitute a genetic entity that differs from both the Atlantic Iberian and Mediterranean populations (Alberto et al. 2008).

In this study, we took advantage of this biogeographical configuration to address whether the resistance and performance of *C. nodosa* to a local perturbation (here, light reduction) varies across three regions within the Temperate Northern Atlantic realm. Specifically, the same experiments, in terms of shading intensity, timing and duration of stressful conditions, were replicated at three seagrass meadows within each of the three regions. We hypothesized that different biogeographical scenarios, which encompass variation in ecological/environmental and genetic conditions, would affect seagrass resistance, in terms of shoot abundance, with implications in the leaf morphology and growth of *C. nodosa*, as well as over seagrass-associated epifauna.

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2. MATERIALS AND METHODS

2.1 Study region and experimental design

This study was undertaken at three regions across the Temperate Northern Atlantic realm (Spalding et al. 2017): Southeast Iberia (Alicante), the Balearic Sea (Mallorca Island), both within the Western Mediterranean eco-region and the Canaries (Gran Canaria Island) within the Macaronesian eco-region in the eastern Atlantic (Spalding et al. 2017) (Figure 1). Despite certain physiological differences between meadows at the Canaries and the Western Mediterranean, intra-regional variation surpasses inter-regional variation in terms of seagrass demography and morphology (Mascaró et al. 2009). Seagrass-associated faunas, on the other hand, differ at regional scales; for example, fish assemblages vary in species richness and composition from the Mediterranean to the Atlantic (Espino et al. 2015). To date, no study has addressed whether the magnitude of herbivory by grazing fishes on seagrass material may geographically differ.

At each region, we selected three seagrass meadows (i.e. locations, situated between ca. 10 and 50 km apart, Table 1, Figure 1). To account for potential intra-regional (local) effects of varying levels of seagrass genetic diversity, we selected the meadows to encompass a gradient of genetic diversity within each region. This strategy accounted for the varying genetic histories of each region, but incorporating local variation in genetic attributes. In this regard, an initial study provided information on the genetic diversity of a range of meadows within each region, which allowed us to select meadows encompassing the entire range of intra-regional variation of genetic diversity (Appendix 1). Sampling, laboratory procedures, clone identification and genetic methods, including a set of nine microsatellite markers (Cy1, Cy18, Cy3, Cy4, Cy16, Cn4-19, Cn4-6, Cn2-38 and Cn2-14), followed Alberto et al. (2003) and Ruggiero et al. (2004). As a result, inter-regional variation in seagrass resistance was not confounded by distinct intra-regional variation in seagrass genetic diversity. Inter-regional

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variation in seagrass genetic attributes, in turn, overpowered intra-regional variation for all genetic attributes (1-way ANOVAs, Appendix 1).

Light manipulations were implemented within 15 plots (1 x 1 m) randomly established in each seagrass meadow; a polyethylene shade cloth was attached to four metal bars perpendicularly inserted into the seabed for each plot. We established three treatments: 'high shading', 'moderate shading' and no shading (procedural control consisting of a plastic 4 cm^2 pore-sized mesh, Appendix 2) with n=5 replicates per treatment. A pilot study (1 week), at the meadow 'Castillo' (Gran Canaria), indicated a decline between one to two orders of magnitude in light intensity within 'moderate' and 'high' shading plots, relative to the procedural control (Appendix 3). We replaced shade cloths (*ca*. 1 m above the bottom) every 3-4 weeks; the experiment lasted 13-14 weeks (between May and September 2017) at each of the nine meadows. Light loggers (Hobo Pendant) continuously monitored total light intensity and temperature immediately above the seagrass canopy within each of three plots, corresponding to each treatment, at each meadow. Despite these devices do not supply PAR, total light intensity and PAR are correlated (Long et al. 2012). Despite large natural fluctuations in turbidity through time from varying environmental (local) conditions, the treatments resulted in significant differences in light intensity between treatments over seagrass canopies (Figure 2; 3-way ANOVA, 'Tr', P=0.00001, Table 2).

2.2 Sampling and laboratory procedures

We assessed seagrass abundance by counting the number of seagrass shoots, at the start and the end of the experiment, by deploying four, 20 x 20 cm, quadrats within each plot. By taking into account initial shoot densities, we estimated the percentage of net change in shoot abundance within each experimental plot (Ceccherelli et al. 2018). We estimated seagrass aboveground growth via the 'punch-hole' method, by piercing 15-20 random shoots

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underwater, at 2 mm above the ligula, within each plot (Terrados & Ros 1992). We pierced seagrass leaves between 12 and 20 days before the end of the experiment. Each pierced shoot was marked with a cable-tie for subsequent collection. At the end of the experiment, we collected most marked shoots, i.e. normally between 12 and 18 shoots per plot. Once in the laboratory, the production of new leaf biomass was then estimated, in terms of increased leaf surface and biomass, by measuring the displacement of the mark for each pierced shoot, and growth calculated per day. Shoot morphological traits (number of leaves per shoot, sheath length, leaf length and width and leaf surface area of each shoot) were concurrently measured for all shoots collected from each plot. In addition, we deployed a 20 x 20 cm quadrat in the center of each plot at the end of the experiment; all aboveground seagrass material, including associated epifauna, were covered and subsequently harvested within a bag. Once in the laboratory, the material of each bag was rinsed with freshwater using a three-rinse cycle; seagrass was agitated to remove the epifauna, water passed through a 500-micrometer mesh sieve, and all epifauna preserved in 70% ethanol. The leaf biomass was separated and oven-dried (60ºC during 48 h) and subsequently weighted. We sorted epifaunal specimens into broad taxonomic units using a binocular microscope and their abundances were then quantified.

2.3 Statistical analysis

Three-way permutational univariate and multivariate ANOVAs (PERMANOVAs) tested for differences in light regimes (daily maximum light intensity), the net change in shoot abundance, seagrass growth and leaf morphometry, as well as total epifaunal abundance and assemblage structure (composition and abundances of all taxa), between regions (fixed factor, 3 levels), shading treatments (fixed factor, 3 levels) and locations (random factor, 3 levels, nested within each region). Morphometry was accounted, within a

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multivariate context, through the five leaf morphological traits considered. We calculated dissimilarities via Euclidean distances from normalized data. In all cases, plots within each light treatment level from each meadow (n=5) were considered as replicates. Transformations, if necessary, were carried out to achieve homogeneous variances, which were accounted by the Cochran's test and the PERMDISP routine for uni and multivariate ANOVAs, respectively (Table 2). For all uni and multivariate ANOVAs, we calculated 'effect sizes' using the partial omega squared index (ω^2_p, Olejnik and Algina 2003). We carried out pairwise tests, when pertinent, to resolve significant effects of fixed factors. Principal Coordinates Ordination (PCO) plots were obtained to visualize multivariate similarities in seagrass leaf morphology and epifaunal assemblage structure between regions, shading treatments and meadows.

A PCO was carried out to visualize similarities between meadows according to their ecological/environmental (mean daily maximum light intensity and sea water temperature during experimentation, depth, meadow area, mean meadow shoot density and grain type, Table 1) and genotypic/genetic attributes (the number of genets, *G*, the clonal richness, *R*, and the standardized allelic richness, $\hat{A}_{38}$, Appendix 1). We initially tested for correlations between each pair of ecological/environmental (Table 1) and genetic attributes (Appendix 1) to limit the inclusion of over-correlated variables ($R^2 > 0.7$) in the multivariate space. This ordination was accompanied by a 1-way PERMANOVA to partition inter- (biogeographical) and intra- (local) regional variation; variance components provided the % of contribution to the total variation by each within and between biogeographical variation. For each meadow, we computed Cohen's *d* 'effect sizes' between controls and high and moderate shading treatments, for the net change in shoot abundance, seagrass growth and leaf morphometry. A matrix of 'effects sizes' was then constructed and similarities between meadows in their overall (i.e. multivariate) 'effect sizes' to simulated light reduction were synthetically

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visualized through a PCO. For each meadow, we then extracted the 'loadings' (coordinates) for component I and correlated, via Pearson-product moment correlation, these coordinates (per meadow) with those provided by the PCO on the ecological/environmental and genetic attributes of the meadows. This strategy specifically tested for a connection between biogeography and seagrass response to shading. To partition the relative roles of environmental and genetic drivers on seagrass resistance, a Generalized Linear Model (GLM) tested whether environmental (depth, area and mean light intensity during experimentation, Table 1) and genetic descriptors of each meadow (the number of genotypes, *G*, and the observed heterozygosity, H_{obs}, Appendix 1), as well as the initial shoot density per plot, significantly affected net changes in shoot density. A Gaussian family of errors with an 'identity' link function was selected to meet the assumptions of linearity and normality of errors, which were checked by a visual inspection of residuals. To select the best predictors, a stepwise procedure with a 'forward/backward' direction was implemented; the AIC provided a criterion to select the most parsimonious model. We implemented multivariate routines in PRIMER 6.0 and PERMANOVA and univariate routines in R 3.4.0.

3. RESULTS

3.1 Seagrass abundance and growth

Experimental shading significantly affected the net change in shoot abundance (3-way ANOVA, 'Tr', P=0.001, Table 2) and was the experimental factor with the largest effect size (ω^2_p= 0.441). Under shading, the percentage of net change in shoot abundance significantly decreased in Gran Canaria relative to the other regions, where shading had a non-significant effect on the net change in shoot abundance when compared with controls (Figure 3; 3-way ANOVA, 'Re x Tr', P=0.001, pairwise tests, Table 2). In Gran Canaria, under high and moderate shading, shoot abundance was *ca*. 5.2 and 3.7 times lower, respectively, than

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controls (Figure 3). However, shoot abundance under high and moderate shading did not significantly decrease, relative to controls, at Alicante (*ca*. 1.5 and 1.2 times, respectively) and Mallorca (*ca*. 1.4 and 1.2 times, respectively) (Figure 3).

Seagrass growth was not affected by experimental shading (Figure 4; 3-way ANOVA, 'Tr' and 'Re x Tr', P>0.1, Table 2), and it inconsistently varied between meadows within each region (Figure 4; 3-way ANOVA, 'Tr x Loc (Re)', P=0.005, Table 2). In turn, the largest 'effect size' on growth was accounted by locations (ω^2_p= 0.041). Seagrass growth significantly varied between regions (3-way ANOVA, 'Re', P=0.023, Table 2), but with a smaller contribution than locations (ω^2_p = 0.026). Seagrass growth was larger in Gran Canaria than the other two regions (pairwise tests for 'Re').

3.2 Seagrass shoot morphology

Overall, seagrass shoot morphology was not affected by experimental shading (3-way PERMANOVA, 'Tr' and 'Re x Tr', P>0.1, Table 2). Seagrass leaf morphology significantly varied between regions (3-way ANOVA, 'Re', P=0.007, Table 2), which accounted for the largest amount of variation (ω^2_p = 0.406). In turn, the PCO revealed an arrangement of locations along the first ordination component (PCO1, Figure 5) according to regions, which accumulated 65.6% of the multivariate variation in leaf morphology. Differences in leaf morphology between shading treatments, on the other hand, varied between locations within regions (3-way ANOVA, 'Tr x Loc (Re)', P=0.014, Table 2). In particular, pairwise tests indicated significant differences in leaf morphology between shading treatments and controls at two meadows (Castillo and Arinaga) from Gran Canaria Island, as indicated by the PCO plot (Figure 5), whereas pairwise differences were non-significant at the two other regions.

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3.3 Epifaunal responses

We identified 14 broad taxonomic units for a total of 1,163 epifaunal organisms (Appendix 4). Shading had no consistent effect over the total abundance and the assemblage structure of epifauna (3-way ANOVA and PERMANOVA, 'Tr' and 'Re x Tr', P>0.1, Table 2). Both the total abundance and multivariate structure of epifauna significantly varied between regions (3-way ANOVA and PERMANOVA, 'Re', P=0.002 and P=0.006, respectively, Table 2), which accounted for the largest amount of variation (ω^2_p = 0.392 and 0.149, respectively). In particular, we observed larger abundances at Alicante than the other two regions (Figure 6, pairwise tests for 'Re'). The PCO showed an arrangement of locations along the first ordination component (PCO1, Figure 7) according to regions, which accumulated 38.7% of the multivariate variation in epifaunal assemblages.

3.4 Connecting biogeographical variation with seagrass resistance and performance

Inter-regional (here, biogeographical) differences accounted for *ca*. 73% of variation between meadows, according to their ecological/environmental and genetic attributes, i.e. only 27% of differences was accounted by intra-regional variation (1-way PERMANOVA). In turn, meadows grouped according to regions in the ordination space, principally along the component I, which accumulated *ca*. 57% of the multivariate variation (Figure 8a). Similarly, meadows clustered according to regions in terms of their overall 'effect sizes' of shading treatments relative to controls (Figure 8b); there was an overlap between certain locations of Mallorca and Alicante as a result of similar responses to shading. The 'loadings' of meadows according to their component I, i.e. from these two PCOs, were significantly correlated (r_s=0.57, P<0.001), indicating that inter-regional (biogeographical) variation was connected with variation in shading effects between meadows.

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The most parsimonious model to explain seagrass resistance included two environmental (light intensity and initial shoot density) and one genetic driver (H_{obs}) (Table 3). The larger the genetic diversity of the meadow, the larger was the final shoot abundance in terms of net changes (coefficient = 216.17, Table 3). Meadows under high light intensity regimes, however, experienced lower increases in shoot abundances (coefficient = -0.0011), and meadows with a high initial density also experienced lower increases in shoot abundances (coefficient = -0.089).

4. DISCUSSION

Seagrass resilience is dynamic with respect to space, time and stressors, varying most strongly with the life history of the seagrass genus and the type, duration and timing of stressors (Soissons et al. 2016, O'Brien et al. 2017). From a theoretical perspective, varying patterns in resistance and recovery of seagrasses occur at a range of scales, from cellular processes at minuscule scales to processes occurring at macroecological scales (Kilminster et al. 2015). A relatively large body of research has addressed resistance of seagrasses to a range of stressors at local-scales. For instance, meadow-specific light regimes and local environmental conditions (e.g. water quality) have affected the response of seagrasses to light reduction (Leoni et al. 2008, Barry et al. 2018). Plants are typically acclimatized to local conditions, and different seagrass species can have a different plasticity to respond to changes in key environmental factors, e.g. light or temperature. *Cymodocea nodosa*, being a plastic species relative to slow-growing seagrasses such as *Posidonia oceanica* (Marín-Guirao et al. 2016), is adapted to shallow or deep-water light conditions along a local bathymetric gradient (Procaccini et al. 2017). In this sense, in our study, meadows under naturally larger light regimens were more susceptible to shading. Importantly, over and above this small-scale variation, our study here has demonstrated significant inter-regional, i.e. biogeographical,

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variation in shoot abundance under light reduction with concurrent, but less accentuated, changes in leaf morphology. The context-dependency of ecological responses to stressors is an idea of long tradition in ecology. However, biogeography has been often overlooked in this regard (Fredston-Hermann et al. 2018). For example, the vulnerability of 'ecosystem engineers' to global change stressors, e.g. warming and ocean acidification, change between distinct biogeographical scenarios (Van Colen et al. 2018, Wernberg et al. 2018). Understanding mechanisms behind this pattern requires integration of biogeography, in terms of varying ecological and evolutionary contexts, but also understanding that the sensitivity of seagrass performance responses may change according to the level of biological organization, e.g. at molecular, shoot, plant or meadow levels (Roca et al. 2016, York et al. 2017, Ceccherelli et al. 2018, Jahnke et al. 2018).

In our study, changes in leaf morphology and, in particular, leaf growth were poor predictors of seagrass decline under stressful shading conditions. In turn, the meadow with a highest growth rate had the largest decrease in net shoot abundance (Castillo). Most likely, this was a morphological response to reach greater light levels and avoid the stressful conditions we experimentally imposed. The inadequateness of these descriptors to describe seagrass degradation, in short-term experiments, has also been recently highlighted (Ceccherelli et al. 2018). These attributes are often more reliable indicators when chronic disturbances act over longer temporal scales (Roca et al. 2016). In general, response time and sensitivity to stressors vary with the type of variable examined, according to the level of biological organization, and the particular seagrass species (Roca et al. 2016). In our study, we initially preferred more integrative seagrass descriptors (shoot density, growth and morphology) over physiological and molecular indicators, as they are effective to track seagrass degradation, particularly for more 'opportunistic' rather than slow-growing seagrass species (Macreadie et al. 2014, York et al. 2017).

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For low dispersal species, as most seagrasses, local adaptation is a prominent mechanism to overcome perturbations, as natural selection is not homogenized by gene flow from populations under different selection pressures (Reusch 2014). *Cymodocea nodosa*, in particular, has low dispersal potential, often up to 10s of m (Alberto et al. 2005, Ruggiero et al. 2005). The colonization of the Canary Islands by *C. nodosa* followed a clear 'founder effect' through the arrival of a few initial migrants (Alberto et al. 2006); this involves colonization from a single source and, therefore, a population 'bottleneck'. Populations of *C. nodosa* in the Canary Islands are peripheral to the distribution range of the species, being close to their western and southern distributional limit (Cunha and Araújo 2009). This geographical configuration promotes genetic isolation from very restricted current gene flow, so allele frequencies principally change through genetic drift, which is reflected in decreased heterozygosity, as this study and Alberto et al. (2006, 2008) have shown. Higher seagrass genetic diversity facilitates resistance to disturbances and environmental stress (Hughes and Stachowicz 2004, Salo et al. 2015), including light depravation (Evans et al. 2017). In our case-study, in particular, we empirically demonstrated that meadows of high genetic diversity (H_{obs}) were more resistant to shading. Mediterranean populations of *C. nodosa* constitute a genetic unit separated from the Canary Islands (Alberto et al. 2008, Masucii et al. 2012). The general gene flow is from the Western and Central Mediterranean towards the Strait of Gibraltar (Masucii et al. 2012). Most likely, this macroecological scenario helps to understand the contrasting resistance of *C. nodosa* to light decrease between regions, in particular between Gran Canaria Island and the Mediterranean regions. Ecosystems where seagrasses are near the edge of their biogeographical ranges may be more vulnerable to stress events (Fraser et al. 2014). Further evidence to support this thesis is not only provided by this study, as resistance of *C. nodosa* to brine release is also notably lower in the Canaries relative to the Mediterranean (Portillo et al. 2014). In turn, this large vulnerability of *C. nodosa* to

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local perturbations has been linked with overall meadow deterioration at the island and archipelago scales (Tuya et al. 2014, Fabbri et al. 2015). Similarly, *C. nodosa* has markedly declined in the adjacent Madeira archipelago (Cunha and Araújo 2009). In summary, seagrasses seem to be particularly vulnerable to local impacts in these oceanic archipelagos, reinforcing the notion that the biogeographic histories of oceanic islands strongly determine the vulnerability of their biotas (Weeks et al. 2016).

Our study has shown that epifauna did not respond, in terms of total abundances and assemblage structure, to light reduction, despite a decrease in the amount of available habitat for epifauna, particularly at Gran Canaria Island. Most likely, more experimental shading time is needed to significantly affect abundances of epifaunal assemblages, as demonstrated experimentally (Gartner et al. 2010). Alternatively, the spatial scale of the shading and its effect on shoot abundance was not relevant for mobile epifauna. These facts have been previously indicated to explain the non-significant implications of short-term experimental seagrass degradation on epifauna, i.e. between controls and disturbed plots (Tuya et al. 2015). Such an artifact should be taken into account, as experiments are context-dependent and limited to short durations, and so may result in conclusions that cannot be entirely extrapolated to a long-term ecosystem scale, particularly when working at the plot-scale (Ceccherelli et al. 2018).

Marine macrophytes (seaweeds and seagrasses) often have intraspecific differences in their niches, resulting from phenotypic plasticity and local adaptation (King et al. 2017). Seagrass populations may differ in their tolerance to stressors across large spatial scales (Bergmann et al. 2010, Salo et al. 2014), which reflect acclimation responses or adaptive genetic differences. Our study suggests that resistance of a seagrass species, here *C. nodosa*, substantially varies across its distributional range and, therefore, that ecotypes, from a resistance functional perspective, may be a common characteristic for seagrasses at local and

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regional scales, as it was hypothesized long ago for other marine macrophytes (Gerard and Dubois 1987). This result expands the recent discovery of local seagrass ecotypes, according to physiological, genetic and genomic criteria (Dattolo et al. 2017, Procaccini et al. 2017, Jahnke et al. 2018), including *C. nodosa* (Marín-Guirao et al. 2016). Functional differentiation particularly occurs for marginal populations of macrophytes (Wernberg et al. 2018), likely resulting from lack of connectivity and restricted gene flow, which has the potential to promote independent evolution of population units (Cánovas et al. 2011). As discussed above, this seems a plausible explanation to understand varying resistance for the seagrass *C. nodosa* across the biogeographical scales considered in this study. This is not trivial, because of potential implications for conservation. Differences in the vulnerability to local disturbances by 'ecosystem-engineers', e.g. seagrasses, should be taken into account to improve conservation plans. Seagrasses, in particular, are included within European conservation legislative bodies, for example within the 'Habitats Directive' (92/43/EEC), which support the Natura 2000 network of European protected areas. From a conservation perspective, larger regional susceptibility to perturbations, in particular, should encourage protection at regional scales to guarantee the persistence of highly vulnerable species. Last, but not least, if resistance differs among biogeographical scenarios, universal conservation rules for seagrasses is challenging.

ACKNOWLEDGEMENTS

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subtidal works at Alicante. This study followed the national rules of Spain and permits were obtained to carry out subtidal experimentation.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.s3r56h1 (Tuya, 2018)

AUTHOR'S CONTRIBUTIONS

FT, YFT, JT, FT conceived the ideas and designed methodology; all authors collected field ecological data; PM, LC, GP performed, analysed and interpreted genetic data, FT analysed data and wrote the paper. All authors contributed critically to the drafts and gave final approval for publication.

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Figure captions

Figure 1. Map showing the position of each location at the Canary Islands (left-hand panel), in the north-eastern Atlantic Ocean, including: (1) Castillo, (2) Gando and (3) Arinaga in Gran Canaria Island, and the western Mediterranean Sea, including: (4) San Juan, (5) Tabarca and (6) Albufereta in Alicante; (7) Formentor, (8) Aucanada and (9) Es Barcarés in Mallorca Island.

Figure 2. Daily maximum irradiation recorded throughout the experiment within plots of 'high' and 'moderate' shading and 'controls' on each of the three meadows from Gran Canaria (a, Castillo; b, Gando; c, Arinaga), Alicante (d, San Juan; e, Tabarca; f, Albufereta) and Mallorca (g, Formentor; h, Aucanada; i, Es Barcarés).

Figure 3. Seagrass shoot abundance at the end of the experiment, in terms of the percentage of change relative to initial conditions, according to experimental shading treatments on each of the three seagrass meadows at (a) Gran Canaria, (b) Alicante and (c) Mallorca. Error bars are +SE of means (n= 5 plots per treatment). A net change in shoot abundance > 100 % denote increased shoot density relative to the start of the experiment. Different letters above bars denote significant differences ($P<0.01$) between treatments for each meadow.

Figure 4. Seagrass shoot growth according to experimental shading treatments on each of the three seagrass meadows at (a) Gran Canaria, (b) Alicante and (c) Mallorca. Error bars are +SE of means (n= 5 plots per treatment). Different letters above bars denote significant differences ($P<0.01$) between treatments for each meadow.

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Figure 5. Bidimensional PCO plot denoting similarities in seagrass leaf morphology between regions, experimental shading treatments and locations within each region. ▼: High shading, ▲: moderate shading, ●: control. Unfilled symbols: Gran Canaria (1, Castillo; 2, Gando; 3, Arinaga), filled symbols: Alicante (1, San Juan; 2, Tabarca; 3, Albufereta), grey symbols: Mallorca (1, Formentor; 2, Aucanada; 3, Es Barcarés). Data are means of 15-20 shoots from each of n=5 plots per treatment.

Figure 6. Total epifaunal abundances, at the end of the experiment, according to experimental shading treatments on each of the three seagrass meadows at (a) Gran Canaria, (b) Alicante and (c) Mallorca. Error bars are +SE of means (n= 5 plots per treatment). Different letters above bars denote significant differences ($P<0.01$) between treatments for each meadow.

Figure 7. Bidimensional PCO plot denoting similarities in epifaunal assemblage structure between regions, experimental shading treatments and locations within each region. ▼: High shading, ▲: moderate shading, ●: control. Unfilled symbols: Gran Canaria (1, Castillo; 2, Gando; 3, Arinaga), filled symbols: Alicante (1, San Juan; 2, Tabarca; 3, Albufereta), grey symbols: Mallorca (1, Formentor; 2, Aucanada; 3, Es Barcarés). Data are means of n=5 plots per treatment.

Figure 8. Bidimensional PCO plots denoting similarities in (a) the ecological/environmental and genetic attributes and (b) 'effect sizes' of shading treatments, relative to controls, of locations (Gran Canaria: Castillo, Gando and Arinaga; Alicante: San Juan, Tabarca and Albufereta; Mallorca: Formentor, Aucanada, Es Barcarés).

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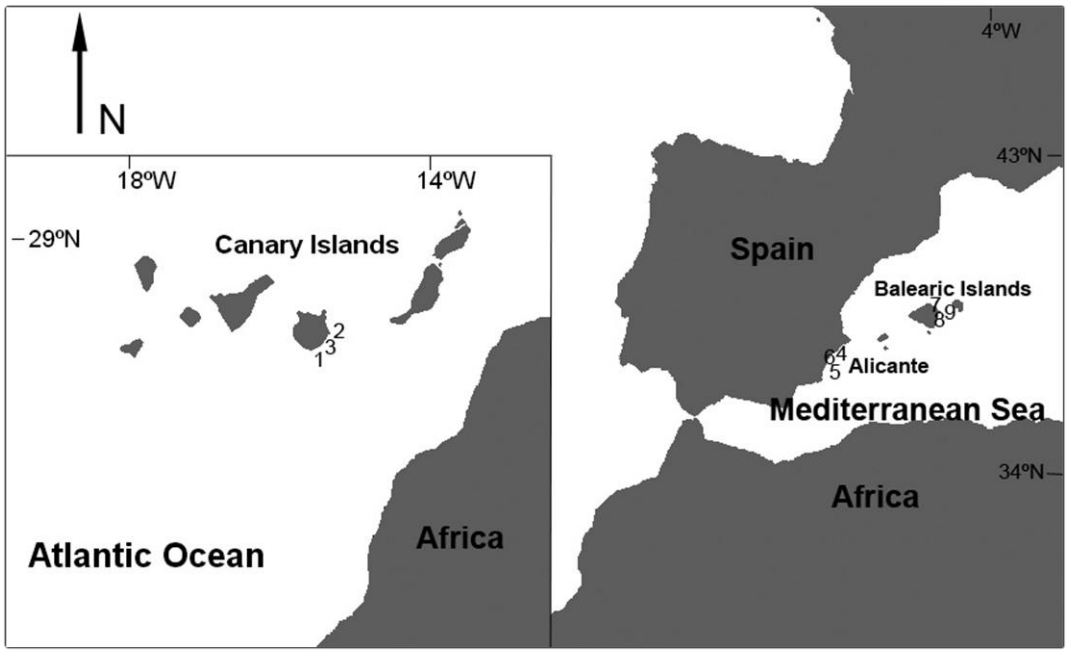

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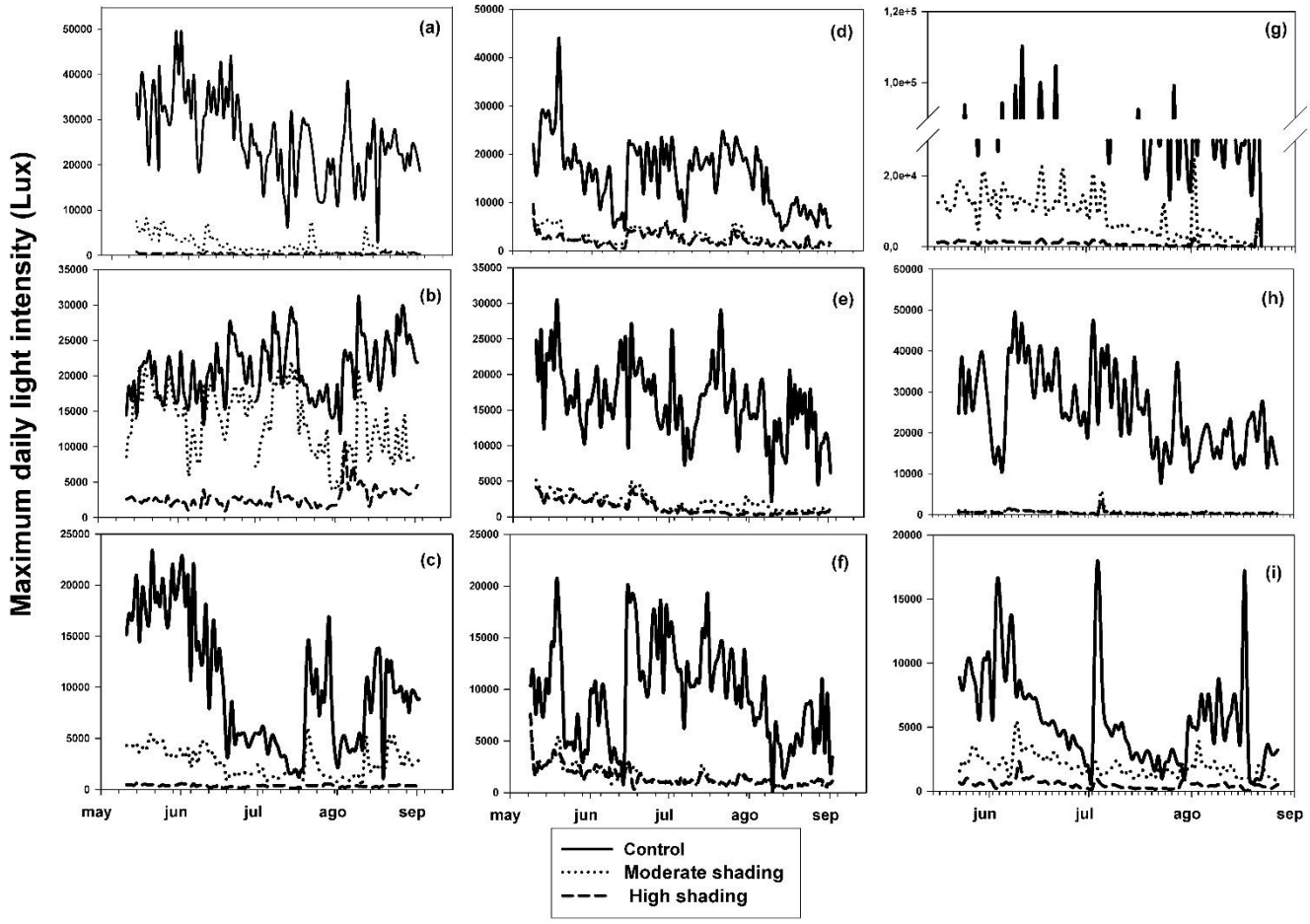

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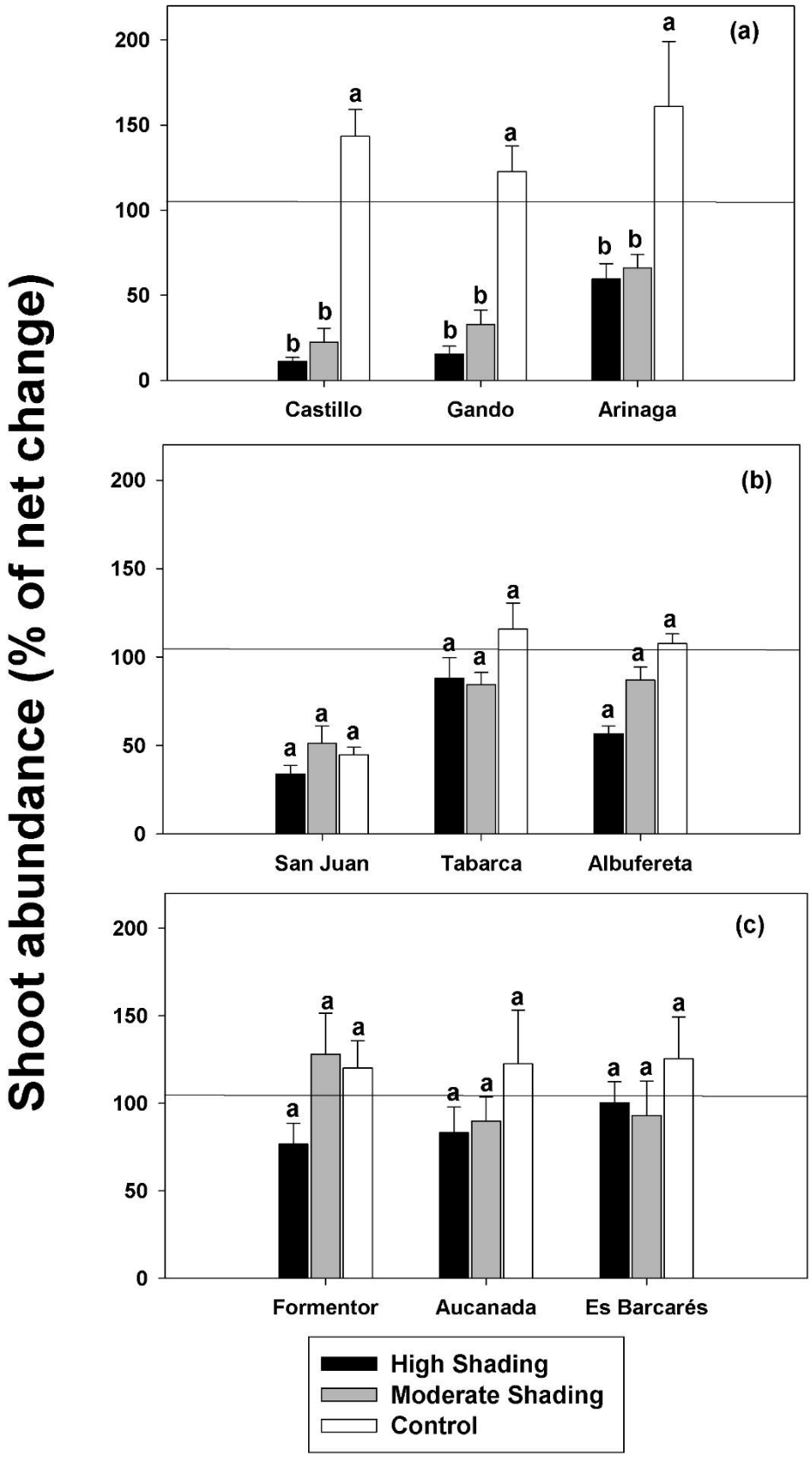

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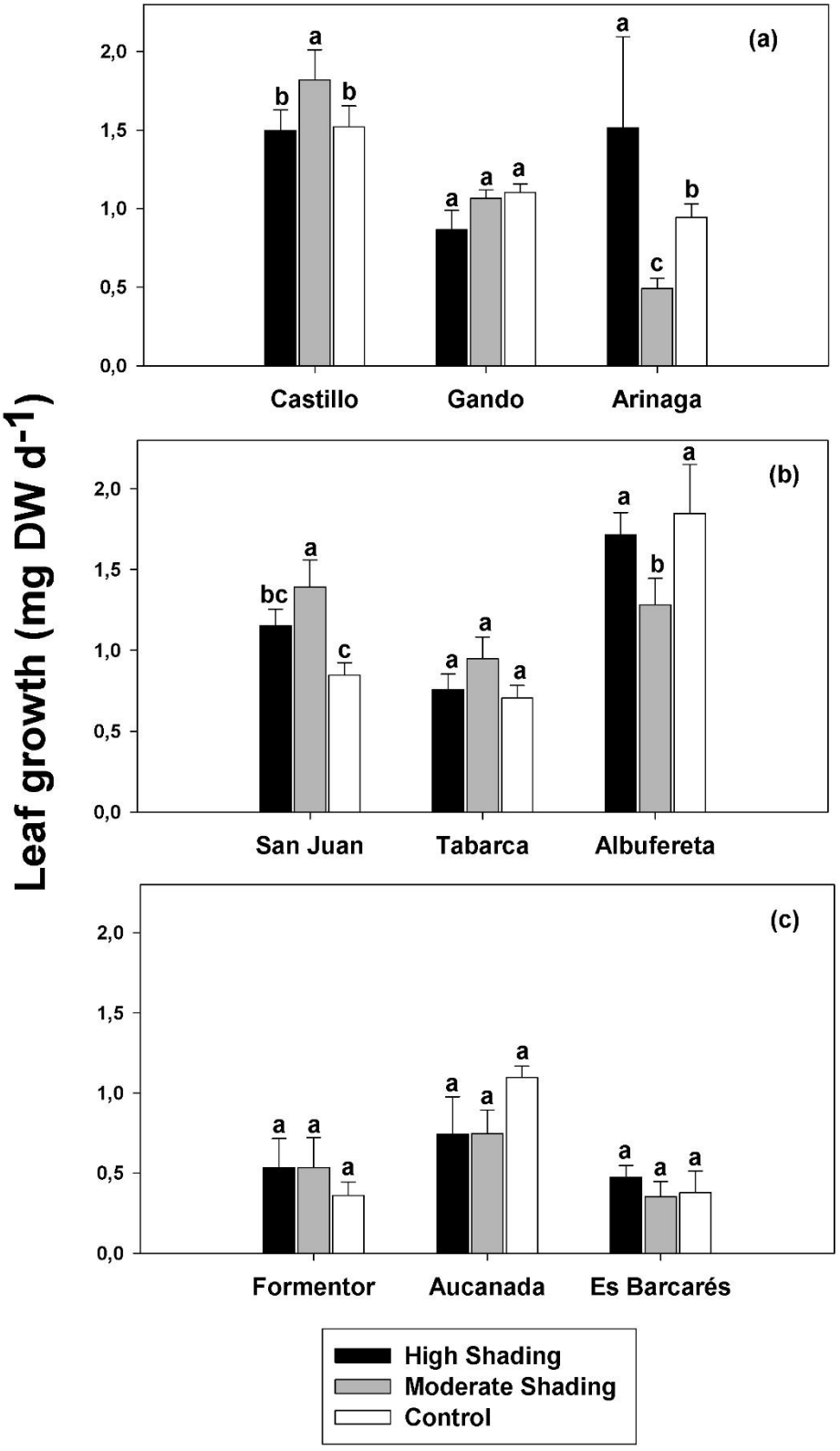

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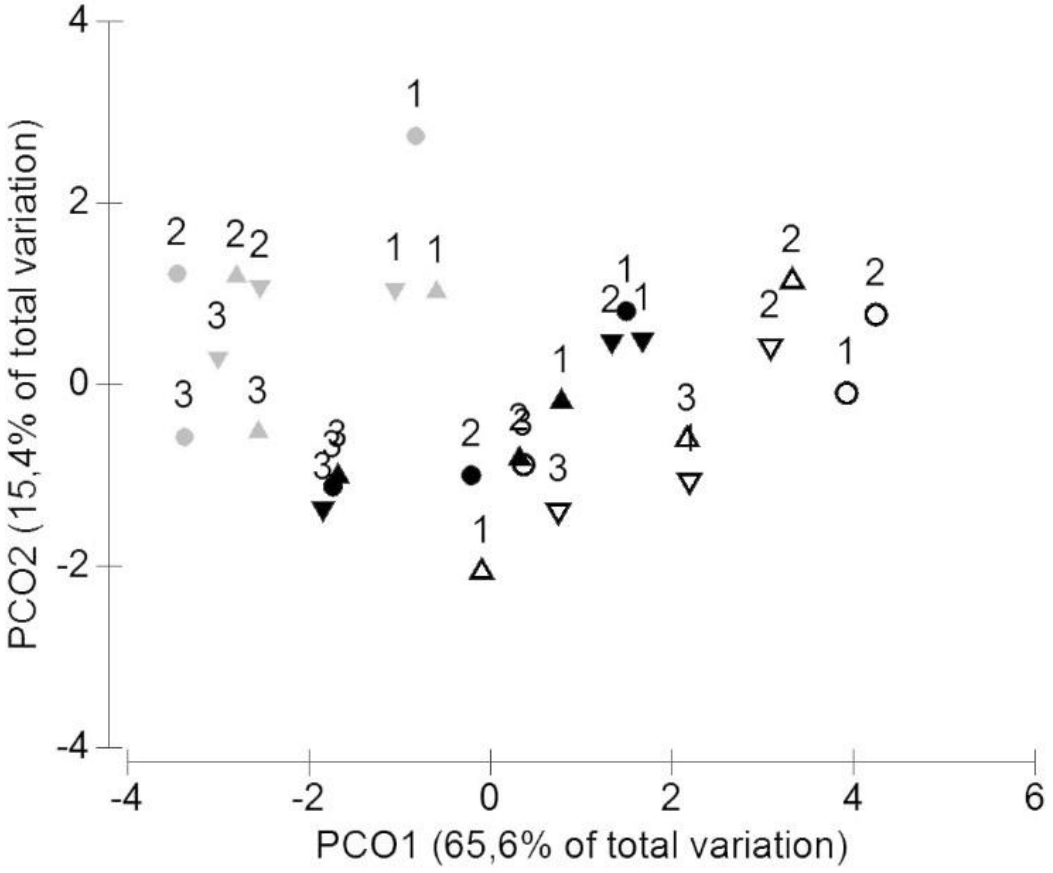

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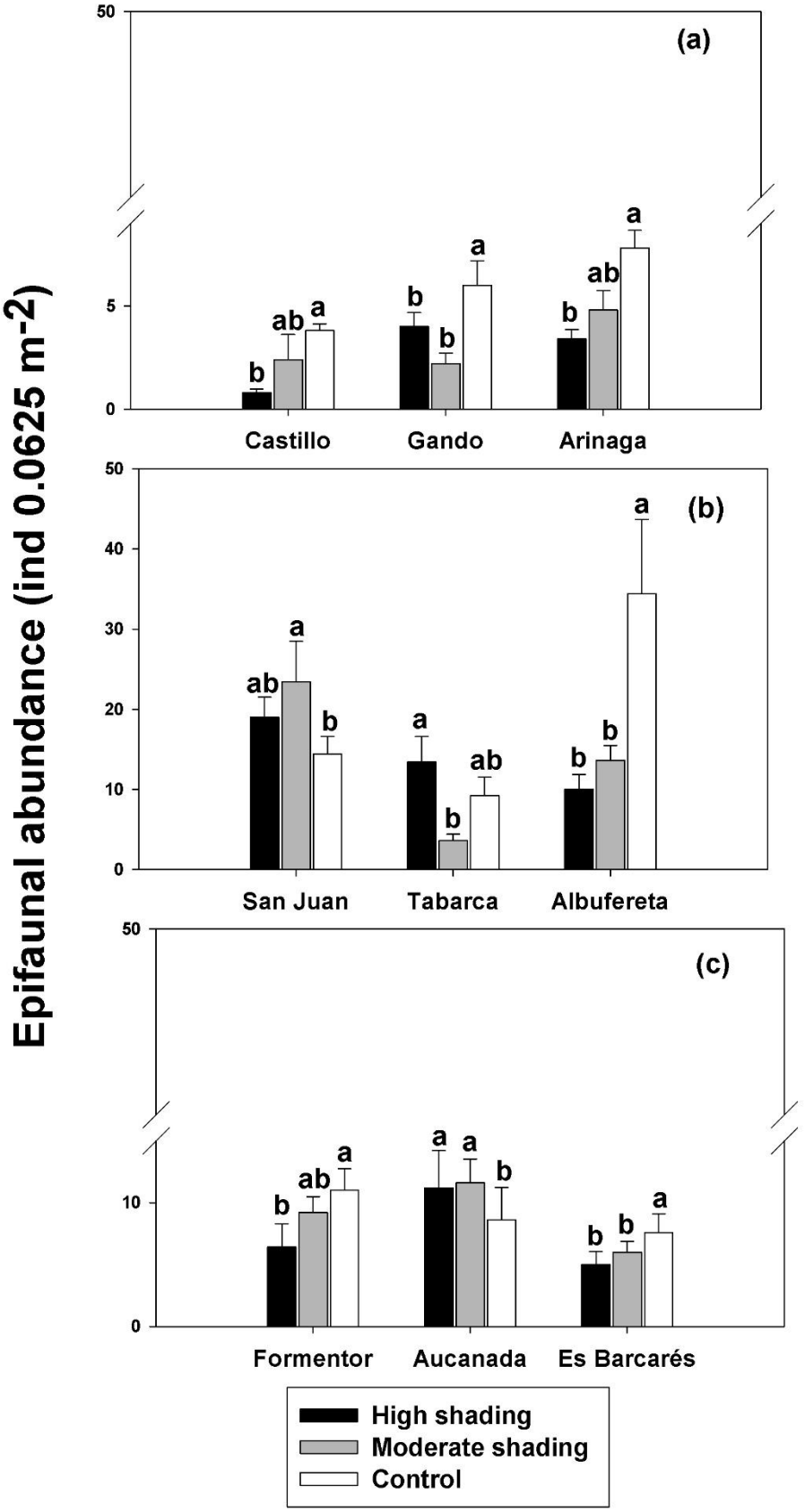

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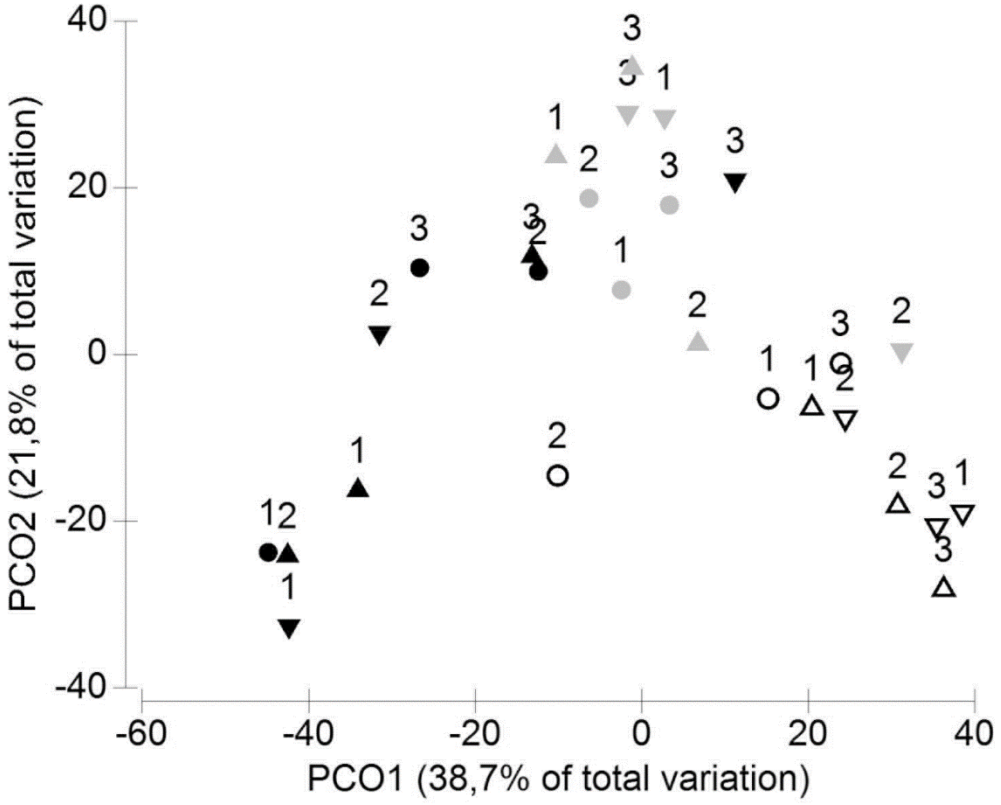

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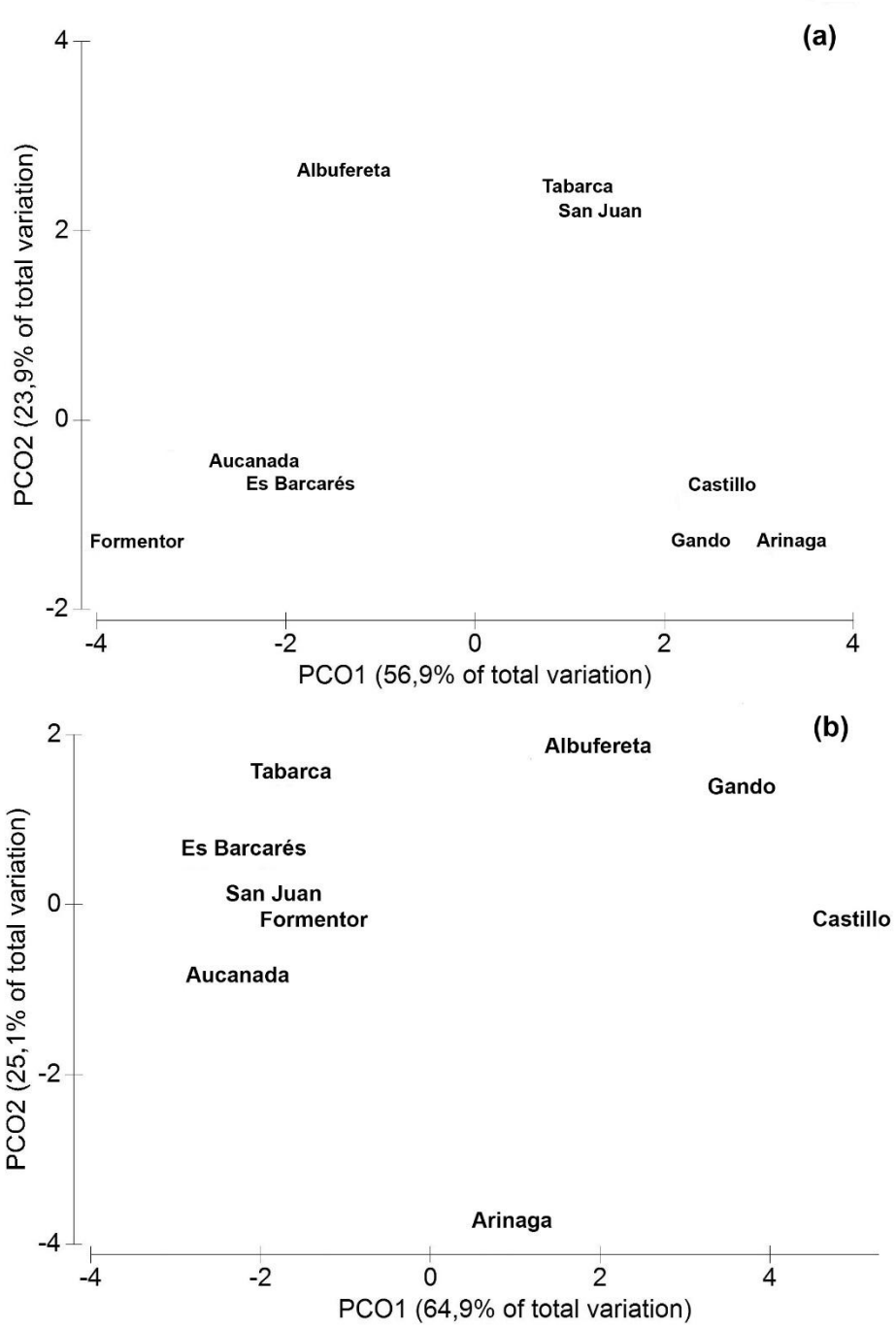

Figure 8

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Table 1. Location and ecological/environmental context of each meadow within each region. 'Light' is the mean of the daily maximum irradiation and 'Temperature' is the mean sea bottom temperature, as measured by HOBO Pendant probes (UA-002-64) immediately above seagrass canopies through the experiment. 'Shoot density' (± SD) is the overall mean of four, 20 x 20 cm, plots deployed within each experimental plot at the start of the experiment (n=60).

	Gran Canaria			**Alicante**			**Mallorca**		
	Castillo	**Gando**	**Arinaga**	**San Juan**	**Tabarca**	**Albufereta**	**Formentor**	**Aucanada**	**Es Barcarés**
Latitude	27°47'16.02"	27°55'29.33"	27°51'6.59"	38°22'59.5'	38°10'02.3"	38°21'00.5'	39°55'38.70"	39°50'13.38"	39°51'36.68"
Longitude	15°29'28.82"	15°22'50.17"	15°23'43.11"	00°23'59.8"	00°30'43.9"	00°26'49.1"	3º8'24.04	3°10'4.58"	3° 6'36.63"
Light (Lux)	26,701.8	20,397.3	10,268.3	44,089	30,311	20,667	48,781	25,541	4,851
Temperature (Cº)	22.58	21.33	21.16	25.24	24.50	25.06	25.61	26.04	27.50
Depth (m)	5	9	10	9	12	10	2.8	2.7	3.5
Meadow area (Ha)	25	5	1.5	380	61	734	0.3	2.2	1.6
Shoot density (m^2)	787 ± 156	654 ± 123	424 ± 83	650 ± 147	1295 ± 258	1005 ± 198	810 ± 188	1183 ± 204	756 ± 188
Grain type	Medium sands	Medium sands	Coarse sands	Fine sands	Fine sands	Fine sands	Fine sands	Medium sands	Medium sands

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Table 2. Results of uni- and multivariate ANOVAs testing for differences in light regimes, the percentage of net change in shoot abundance, seagrass growth and morphometry, as well as total epifaunal abundance and assemblage structure, between regions, shading treatments (HS: 'High Shading', MS: 'Moderate Shading' and C: 'Control') and locations within each region. Significant P-values are highlighted in bold. ω^2_p is the partial 'effect size' of each term. Transformations to achieve homogeneous variances are indicated, as well as the outcomes of the Cochran's (C) test and the PERMDISP routine for uni- and multivariate ANOVAs, respectively. Pairwise tests are included for fixed factors.

Light regimes					
C= 0.1025 (P= 0.3, Ln(x+1))	df	MS	F	P	ω^2_p
Re = Region	2	43.2	0.32	0.7395	0.085
Tr = Treatment	6	136.1	391.19	**0.0001**	0.470
Loc (Re)	2	2017.7	51.80	**0.0001**	0.814
Re x Tr	4	62.4	1.60	0.2367	0.213
Tr x Loc (Re)	12	38.9	111.96	**0.0001**	0.335
Residual	2673	0.3			
Pairwise tests	'Tr': C > MS > HS				

% of net change in shoot abundance					
C= 0.1229 (P> 0.1, √ x)	df	MS	F	P	ω^2_p
Re = Region	2	67.2	2.62	0.093	0.261
Tr = Treatment	2	146.5	37.41	**0.001**	0.441
Loc (Re)	6	25.7	9.50	**0.001**	0.274
Re x Tr	4	48.4	12.35	**0.001**	0.333
Tr x Loc (Re)	12	3.9	1.45	0.156	0.038
Residual	108	2.7			
Pairwise tests	'Re x Tr': Gran Canaria: HS=MS < C, Alicante and Mallorca: HS=MS = C				

Leaf growth					
C= 0.11153 (P> 0.1, √ x)	df	MS	F	P	ω^2_p
Re = Region	2	3.2261	9.91	**0.023**	0.026
Tr = Treatment	2	7.73E-03	0.13	0.878	0.014
Loc (Re)	6	0.32545	15.01	**0.001**	0.041
Re x Tr	4	1.35E-02	0.23	0.921	0.001
Tr x Loc (Re)	12	5.95E-02	2.74	**0.005**	0.056

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		2.17E-02			
Residual	108				
Pairwise tests	'Re': Gran Canaria > Alicante = Mallorca				

Leaf morphometry

F: 2.8128 (P> 0.05, no transformation)	df	MS	F	P	ω^2_p
Re = Region	2	130.4	4.64	**0.007**	0.406
Tr = Treatment	2	3.2	0.68	0.67	0.002
Loc (Re)	6	28.1	10.17	**0.001**	0.290
Re x Tr	4	3.6	0.77	0.651	0.009
Tr x Loc (Re)	12	4.6	1.68	**0.014**	0.057
Residual	108	2.8			
Pairwise tests	'Re': Alicante > Gran Canaria= Mallorca				

Total epifaunal abundance

C= 0.1393 (P> 0.05, log (x+1))	df	MS	F	P	ω^2_p
Re = Region	2	1738.4	8.49	**0.006**	0.392
Tr = Treatment	2	57.9	0.35	0.718	0.008
Loc (Re)	6	204.8	5.53	**0.001**	0.156
Re x Tr	4	73.3	0.45	0.783	0.026
Tr x Loc (Re)	12	162.6	4.39	**0.001**	0.203
Residual	108	37.0			
Pairwise tests	'Re': Alicante > Gran Canaria= Mallorca				

Epifaunal assemblage structure

F: 2.00 (P> 0.1, no transformation)	df	MS	F	P	ω^2_p
Re = Region	2	27509.0	3.583	**0.002**	0.149
Tr = Treatment	2	3337.2	1.36	0.224	0.006
Loc (Re)	6	7678.4	3.75	**0.001**	0.093
Re x Tr	4	2078.3	0.85	0.652	0.000
Tr x Loc (Re)	12	2440.7	1.19	0.134	0.000
Residual	108	2046.6			
Pairwise tests	'Re': Alicante ≠ Gran Canaria= Mallorca				

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Table 3. Results of the GLM to partition the relative roles of environmental (depth, area, mean light intensity and initial shoot density per plot, Table 1) and genetic drivers (the number of genotypes, *G*, and the observed heterozygosity, H_{obs}) on seagrass resistance.

Model: net.change ~ initial.shoot + H_{obs} + light				
AIC: 1421.7	DF	Deviance	AIC	Coefficients
None		252366	1421.7	
- Light	1	277428	1429.6	-0.0011
- initial.shoot	1	3148712	1446.7	-0.089
- H_{obs}	1	328130	1452.3	216.17
Null Deviance		343600		

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